Explanation of Abbreviations in Text-figures.

Abd.c. Abdominal cavity.
A.int.as. Anterior intermediate air-sac.
Cf. Line of fusion of cœlomic epithelium of post-pulmonary septum with that of lateral body-wall.
Ct.pl.m. Costo-pulmonary muscles.
D.ms. Median dorsal mesentery.
D.pl.lg. Dorsal pulmonary ligament.
Gz. Gizzard.
Ht. Heart.
Kd. Kidney.
Lng. Lung.
Lv. Liver.
Ml.dt. Müllerian duct.
Ob.lg.lv. Oblique ligament of the liver.
Œs. Œsophagus.
P.as. Posterior air-sac.
Pc. Pericardium.
P.hp.c. Post-hepatic cavity.
P.hp.spt. Post-hepatic septum.
Ph.rs. Pulmo-hepatic recess.
P.int.as. Posterior intermediate air-sac.
Pl.c. Pleural cavity.
Pl.hp.c. Pulmo-hepatic cavity.
Pl.rt. Pulmonary rudiment.
P.pl.spt. Post-pulmonary septum.
P.p.p.m. Pericardio-pleuro-peritoneal membrane.
Prn.fd. Pronephric fold.
Pt.c. Peritoneal cavity.
Spl. Spleen.
Sp.rnl. Supra-renal body.
St. Stomach.
Um. Umbilical opening.
V.lv.s. Ventral liver-sac.
V.ms. Median ventral mesentery.
V.pl.lg. Ventral pulmonary ligament.
Wf.by. Wolffian body.

2. The Growth of the Shell of *Patella vulgata* L.

By E. S. Russell, M.A.*

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(Plate XXXII.†)

This paper consists of two parts; the first a study of the rate of growth of the limpet-shell, the second a study of the gradual change in the shape of the shell as it grows in size. Throughout the paper the *size* of the shell has been taken as a measure of its growth. Owing to the manner in which growth takes place, no dimension of the shell can increase without a corresponding increase in the other dimensions, so that any one dimension may be taken as a measure of growth, *i. e.* of increase in size. It is convenient to take length as a measure of size. Knowing the length one can calculate with a fair degree of accuracy all the other dimensions, if one has previously determined the average ratios of the other dimensions to length for successive values of the length.

I. Rate of Growth.

1. *Breeding Season.*

The fact that limpets of 5 mm. in length may be found in January and in July leads one to suppose that the breeding season is of considerable duration, and the observations which I have made fully confirm this opinion.

I tried to discover at what time of year small limpets chiefly appear, by watching events in the small bay where I studied the growth of the limpet. On January 11th, 1908, there was a

* Communicated by Prof. J. Arthur Thomson, F.Z.S.
† For explanation of the Plate see p. 253.

small proportion of 10–15 mm. shells and on January 25th there was seemingly a greater proportion of small shells 7–10 mm. in length. After that I have no records which indicate the settling down of very young limpets until July 21st, when I found that the small shells were mostly 15–25 mm. in length (and therefore simply the descendants of the 10–15 mm. long limpets of January), but that an occasional small one (8 mm.) occurred among them.

On August 4th at Millport I collected one or two tiny shells 2·5–3 mm. long from the crevices of a rock in the lower half of the beach. On September 2nd at the Cloch, Gourock, there were visible in the bay a few 5–10 mm. shells, and on October 1st there were a few shells 8–12 mm. in length in places where they were not present on September 2nd.

From these data it would appear that the breeding-season extends from July to December or January. I examined also the gonad of a number of limpets at various times during the year.

On September 18th, 1907, three limpets were examined. Two of them were females, 28 mm. and 40 mm. in length, and the ovaries contained large but not quite ripe ova. In the 40 mm. long male the spermatozoa were fairly ripe. A number collected at the Cloch on December 25th, 1906, were quite ripe. Of 26 limpets collected at Cardwell Bay, Gourock, on December 28th and 31st, 1907, 21 were males and only 5 were females. The males were not very ripe and some of them seemed spent, but the females had mature sexual products. Of five males collected at the Cloch on January 11th, 1908, only one was at all ripe, the others being spent. Ten limpets, 4 females and 6 males, were taken on February 8th. The males seemed spent and the ova in the gonads of the females were disintegrating. The breeding season is clearly over by the end of January if not a little sooner.

The sex of six limpets of 35–42 mm. in length collected on the 23rd May could not be determined with certainty, though they appeared to be males. The gonad was brick-red and only one-half to three-quarters its full size. At the anterior end it was beginning to turn cream-coloured, as if it were ripening into a mature testis in that region.

A male examined at Kames on July 2nd, 1906, had well-developed spermatozoa.

On July 11th, eleven limpets were examined. Six of them were females and their ovaries were at all stages of ripeness. One or two showed a number of fairly ripe ova, and the ovary had the typical olive-green tint which it shows when at all mature. The others were extremely unripe with very minute ova, and the colour of the ovary was a reddish-brown. The males were all moderately ripe. I attempted to carry out artificial fertilisation, and rather to my surprise obtained a number of early segmentation stages.

Artificial fertilisation was carried out with success at Millport on August 4th, early segmentation stages being again obtained.

Of 23 limpets collected at the Cloch on October 1st, 19 were males and fairly ripe, 3 were females also ripe, and 1 was immature, being only 20 mm. in length.

The breeding-season, therefore, probably lasts from about the middle of July to the middle of January. There is much individual variation as to the time of ripening, and so it is improbable that any single limpet is mature throughout the whole breeding-season. While the commencement of the breeding-season seems to be ill-defined, its finish is more definitely fixed.

Dr. J. F. Gemmill, who has examined the gonads of many limpets, tells me that he considers the limpet to be ripe from the beginning of November to the first fortnight of January. Davis and Fleure write (2. p. 59), "the season of sexual maturity is the autumn; Boutan finds it to be about September at Roscoff; at Aberystwyth we think it is somewhat later."

According to Fischer (3. p. 867) "la ponte s'effectue sur les côtes océaniques de France à la fin de mars et au commencement d'avril," which agrees well with the observations detailed above. It is probable that on our own shores the limpet is ripest during the months of October, November and December. A similar state of affairs seems to hold in the Adriatic, for Patten (8) obtained artificial fecundation of the eggs of *Patella* at Trieste in the beginning of December and the middle of January. At Naples, however, Wilson found the eggs of *Patella cærulea* in a mature state from March until June (12. p. 199).

Size at which maturity is reached.—From the examination of a large number of limpets (80–90)'I find that sexual maturity is reached by the males at a length not less than 21 mm. I have found immature males during the breeding-season 16·5, 19·5, 20, and 21 mm. long. The gonad grows with the animal, and in males 21–30 mm. in length it is only about half its ultimate size. It is fully developed at about 40 mm.

I have seen no female smaller than 26 mm., but at that length the limpet may have mature ova. The ovary attains its full size in limpets of about 40 mm. in length.

According to Dr. Gemmill's observations limpets may be mature as small as 18–20 mm.

It is of interest to compare the closely allied *Acmæa* with *Patella* in this respect. In *Acmæa* (the breeding-season of which lasts from the middle of April to the end of July) sexual maturity is attained under 10 mm. long and probably after one winter (Willcox, 11).

Another interesting example from among the Gastropoda of a very rapid attainment of sexual maturity long before adult size is reached is to be found in Semper's 'Animal Life' (p. 126). Land snails in the warm regions round the Mediterranean are brought to sexual maturity when only six months old by the heat and moisture of the spring. They are then by no means full-grown.

Proportion of the Sexes.—Out of 87 limpets examined, 66 were

males and 21 females. They were collected for the most part near Gourock. The males are apparently about three times as numerous as the females in this locality, while at Millport Dr. Gemmill (5. p. 394) found that of about 250 limpets examined 68 per cent were females. From some old observations by Lebert and Robin (6) it appears that in their experience there were about three males to eight or ten females. It would be interesting to discover the reason for this great variation in the proportion of the sexes.

2. *Growth Data.*

In order to study the rate of growth of the limpet throughout the year I marked a considerable number on December 31st, 1907, in a bay near the Cloch, Gourock, and attempted to keep full records of their growth from month to month during 1908. A number of them of course disappeared during the year, but their places were filled by others; for example on May 25th and May 30th, I measured about two dozen small-sized limpets and kept many of them under observation until the end of the year.

The detailed records are given in Table I. where they are arranged in year-groups, and more or less in order of magnitude in each group. M = mean value.

The possibility of arranging the measurements in year-groups, at least for the first two years, arises from the fact that the breeding-season of the limpet, though a very long one, is fairly well-defined.

TABLE I.—*Growth-Data, arranged in Year-Groups.*

1908 brood, Oct. 31, 11·5 mm. Nov. 30, 13 mm.

FIRST YEAR-GROUP (1907 brood).

	1907 Dec. 31.	1908 Jan. 25.	Feb. 8.	Mar. 14.	Apr. 14.	May 23.	May 25.	May 30.	June 27.	July 30.	Sep. 2.	Oct. 1.	Oct. 31.	Nov. 30.	Dec. 31.
1...	...	...	9·6	10·2	12	14·5	...	...	18·7						
2...	...	10	...	...	11·9	14·5									
3...	...	...	10·4	11	12·5	15·3	...	...	18·9	19·8	23·7	26	27·6		
4...	...	...	10·5	11·5	13·1	16·8	...	...	21·5	23·8	27·1	31			
5...	...	...	11·1	12	...	16·4	...	...	20·8	22·6	26·3	28	29·3		
6...	...	...	...	...	...	...	...	10·3	13	14·9	19·1				
7...	...	...	...	...	...	...	10·9	...	14	16	..	20·2	21	21·1	
8...	...	...	...	...	...	...	12	...	14·5	17·1	20	22	23		
9...	...	...	...	...	...	...	...	11·9	14·9	18·2	20·8	22·5			
10...	...	...	...	...	...	...	11·6	...	15						

FIRST YEAR-GROUP (1907 brood) (*continued*).

	1907 Dec. 31.	1908 Jan. 25.	Feb. 8.	Mar. 14.	Apr. 14.	May 23.	May 25.	May 30.	June 27.	July 30.	Sep. 2.	Oct. 1.	Oct. 31.	Nov. 30.	Dec. 31.
11...	...	...	...	...	...	...	10·8	...	15	20					
12...	...	...	...	...	...	...	...	13	15·1	18·4	21·9	24·3			
13...	...	...	...	...	...	...	13	...	15·8	18·3	21·9	24·3	26	27·3	27·3
14...	...	...	...	...	...	...	13	...	16	18·8	22·4	25			
15..	...	...	...	...	...	...	14·4	...	16·4	19·1	21	23·4	24·5	26·2	27
16...	...	...	...	...	...	...	...	14·5	16·6	17	20	22·9	24·5	24·5	24·5
17...	...	...	...	...	...	...	...	14	16·9	21	24	26·4	27·2	27·8	28
18...	...	...	...	...	...	...	13·3	...	16·9	20·9	23·5	25·8	27·1		
19...	...	...	...	...	...	...	13	...	17·1	21·9	24·5	27·8	29	29·8	30
20...	...	...	...	...	...	...	15	...	...	19	21·3				
21...	...	...	...	...	...	...	15·5	...	17·7	21	24·5	26·4	28		
22...	...	...	...	...	...	...	...	16·1	18·5	22	25·4	26·5	27·9	28·7	28·9
23...	...	...	...	...	...	...	...	16	19	21·5	24·7	26·8	29	29·9	29·9
24...	...	...	...	...	...	...	...	18	19·2	22·8	25	27·5	28·9	29·1	29·7
25...	...	...	...	...	...	...	16·4	...	19·5	23	26·6	27·8	28·5	29·2	29·2
26...	...	...	...	...	...	...	17	...	19·5	23	26·8	28			
27...	...	...	...	...	...	...	15·9	...	19·7	24	26·1	28·5	29·9	30·5	31
28...	...	...	...	...	...	...	16·8	...	19·9	21·1	22·1	23	23·2	25	25
29...	...	...	...	...	...	...	19·6	...	22	25·4	27	28·1	28·8	29·2	29·2
30...	...	...	...	...	...	...	...	18·8	22·1	24·1	28	29·3	30·9		
31...	...	...	...	...	...	...	...	19·8	23·5	27·2	30·5	32·8	33·1	33·8	33·8
32...	...	...	14	14	15·2	18									
33...	...	...	14·2	14·6	16·7	18·9	...	...	21·7	25·2	28·2	31	32·4	34·5	
34 ..	...	...	...	15·3	16·5										
35...	...	...	...	...	...	...	...	...	...	...	25·1	26·1	27·3		
36...	...	...	...	...	...	...	...	...	...	...	...	29·5	30·9		
37...	...	...	17·6	18·2	18·6	22	...	...	24·2						
38...	...	...	...	18·8	19·9	21	...	...	24·5	27·8	29·8	31·6	...	...	33·4
39...	...	...	...	...	21	22·5	...	...	25·3	...	28·7	29·5	30·5		
M...	...	...	...	...	...	15·5			18·6	21·2	24·5	26·7	27·8	28·4	29·1

Second Year-Group (1906 brood).

	1907 Dec. 31.	1908 Jan. 11.	Feb. 8.	Mar. 14.	Apr. 14.	May 23.	June 27.	July 30.	Sep. 2.	Oct. 1.	Oct. 31.	Nov. 30.	Dec. 31.
40 ...	...	21	21·8	22·2	23·1	23·6	26·7	28·6	30·4	30·8	32·4	32·5	33·5
41 ...	...	21·3	22·1	22·2	23	24·3	26·2	27	28				
42 ...	...	23·7	25·1	25·5	26·2	26·6	27·8	29·3	30	31			
43 ...	22	...	22										
44 ...	22·5	...	23	24·1	25·6	26·8	29·1	31·2	34·4		35·3		
45 ...	23·8	...	24·1	24·6									
46 ...	25·5	...	26	26·9	27·2	28·4	29·8	32·9	35·6	36·7	37	37	37
47 ...	27	...	27	27·5	28·2	29	30·8	33	34·2	34·8	35·2	35·2	35·3
48 ...	27·9	...	...	...	28·8								
49 ...	...	27·2	27·7	28	28·5	28·5	30·2	30·8	31	31·2	33	33·3	33·6
50 ...	29	...	29	30	31	31·1	31·8	34	36	36	37	37·2	38
51*...	...	...	29·1	...	...	32	34·5	...	37·9	39·5	40		
52 ...	29·2	...	29·9										
53 ...	...	...	29·9	...	30·5								
54 ...	30	...	31	...	...	32·9	34	36·9	38	38·9	38·9		
55 ...	30	...	...	...	...	33·4	35·4	37·9	39·2	40·5	42	42·2	42·2
56 ...	30·5	...	31	...	32	32·9	32·9	35	37·8	39	39	39	39
57 ...	...	...	32·5	32·8	33·6	34·5	37·4	40·8	42	42	42	42	42·2
58 ...	...	32·4	32·8	33·6	34	35	37·6	40·1	40·9				
59 ...	...	32	33	33	33·3	34							
60 ...	32·6	...	33	33	34	34·8	36·5						
61 ...	33·4	...	34·2										
62 ...	33·5	...	...	34	35	35·7	36·9						
63 ...	34·4	...	35·9										
64 ...	...	...	...	...	...	36·8	38·4	...	40·8	41	41	41	41
65 ...	...	...	...	...	...	...	...	...	40·6	40·8	41	41	
M ...	28·8	...	28·6	28·4	29·6	31·1	32·7	33·7	36	37·1	38	38	38

* No 51 measured 23·5 mm. on 7th Sept. 1907.

THIRD YEAR-GROUP (1905 brood).

	1907 Dec. 31.	1908 Jan. 25	Feb. 8.	Mar. 14.	Apr. 14.	May 23.	June 27.	July 30.	Sep. 2.	Oct. 1.	Oct. 31.	Nov. 30.	Dec. 31.
66 ...	36	...	36	...	37·1	38·7	40·1	...	43·8	44	45		
67 ...	36·4	...	...	37·9									
68 ...	36·7	...	36·9	...	37·2	37·9	38·9	38·9	38·9	38·9	39	40	40
69 ...	38·1	...	...	39	39·5	40	41						
70 ...	...	37	...	37·5	37·5								
71 ...	...	...	...	...	...	...	...	...	42	43	43·2	43·2	43·2
72 ...	...	...	...	...	...	...	...	...	43·2	44	44	44	44
73 ...	...	...	...	...	...	...	...	...	44	45·5	45·5		
73*a*...	...	...	...	...	...	40	41	...	42·8	43·5	43·9	43·9	43·9

FOURTH YEAR-GROUP (1904 brood).

	1907 Sept. 7.	Dec. 31.	1908 Jan. 11.	Feb. 8.	Mar. 14.	Apr. 14.	May 23.	June 27.	July 30.	Sep. 2.	Oct. 1.	Oct. 31.	Nov. 30.	Dec. 31.
74 ...	43·5	46·8	...	46·8	47·1	47·4								
75 ...	...	43	...	43·9	44	44								
76 ...	43·6	46	...	46	...	46	46	47	...	47·9	48	48	48·1	48·1
77 ...	45·7	46	...	46	46									
78 ...	...	...	45	45	45·5									
79 ...	46·5	...	...	47	47	47·6								
80 ...	...	...	...	...	...	...	...	...	...	47·4	47·5	47·5	47·5	47·9
81 ...	...	...	...	...	...	...	...	...	...	49·2	49·2	49·3	49·3	

FIFTH OR SIXTH YEAR-GROUP (1903 or 1902 brood).

82 ...	...	50	...	...	50	50	50							
83 ...	50	50·5	...	50·5	51	51·4	52	52·2	...	52·5	52·5	53	53·5	53·5

First Year-Group.—It is a curious fact that one rarely finds on the shore limpets less than say 7 mm. long. I have found them of

5 mm., 4 mm., and 2·5 mm. in length, but such small limpets are distinctly rare. They are of course extremely inconspicuous. In the autumn and during the winter limpets of about 10 mm. long gradually appear on the shore, settling down in greatest abundance in the months of January and February. There seems no reason to doubt that such limpets are only a few months old, and represent the first year-group. As the tables show they grow very rapidly (see Tables I. and V.) and can have taken only a few months to reach the length of 10 mm. It should be noticed that in very small limpets (2—3 mm.) the shell is very much larger in proportion to the animal than in older limpets. If these limpets of about 10 mm. length represented not the first but the second year-group there ought to be found on the shore in spring and summer great numbers of shells from about 3 mm. to 7 mm. in length, and this is quite certainly not the case. Nor does it seem likely that the free-swimming larval life of the limpet is very long, or indeed longer than a week or two, for in the allied *Acmæa virginea* the pelagic life is limited to a few days (Boutan). *Acmæa testudinalis*, a much smaller shell than *Patella vulgata*, breeds from April to July and the season's young are 4–5 mm. long in October (Willcox, 11).

A random sample of 1003 limpets taken in July 1903 and 1904 at Southend, Arran, show very clearly that this group of shells about 10 mm. long in January is really the first year-group. The sample was taken just at the very beginning of the breeding-season so that only a very few of the season's young were included.

Table II.

Random Sample in month of July.

Size in mm.	No.	Size in mm.	No.
3— 5·5	5	36—38·5	60
6— 8·5	9	39—41·5	50
9—11·5	26	42—44·5	65
12—14·5	72	45—47·5	91
15—17·5	102	48—50·5	83
18—20·5	97	51—53·5	77
21—23·5	55	54—56·5	39
24—26·5	38	57—59·5	12
27—29·5	41	60—62·5	4
30—32·5	41	63—65·5	1
33—35·5	34	66—68·5	1

The first year-group revealed by these figures has its mode clearly in the fifth class (15–17·5 mm.). Leaving out the first class (3–5·5 mm. shells), which represents probably the first of the season's brood, and taking the next seven we find that the mean value is 17·53 mm., indicating that limpets of the last season are

now in July of an average length of 17–18 mm. These facts taken together seem to warrant us in placing in the first year-group the limpets, Nos. 1–5 (Table I.). These reach a length of about 15 mm. by the third week in May. Nos. 6–31 form a natural group, since they were all found in a small area of a few square yards and present no abrupt difference in size. Nos. 6–23 are quite clearly of the same year-group as Nos. 1–5, and it seems safe to include also in this first year-group Nos. 24–31 and 32–36. No. 29 for example, though 19·6 mm. long on May 25th, is only 29·2 mm. long on Dec. 31st, a length which is reached on that date by No. 25 which was only 16·4 mm. long on May. 25th. One must allow for a good deal of variation in the rate of growth as well as for the fact that each year-group may include limpets differing as much as six or seven months in age, since the breeding-season is of that length. Nos. 27 and 28 illustrate how one limpet may differ from another in rate of growth, so also do Nos. 3 and 4. On the other hand the rate of growth often exhibits surprisingly little variation, as is shown by Nos. 12, 13, and 14, 17 and 18, 24 and 25, and others.

The placing of Nos. 37, 38, and 39 in the first year-group is a little doubtful, but is I think on the whole justifiable.

The mean values have been calculated from the month of May onward, and from them we can infer that a limpet which has come into existence say in September will reach a length of about 15 mm. in the following May, 18 mm. in June, 20 mm. in July, 24 mm. in August, 26 mm. in September, 27 mm. in October, 28 mm. in November, and by the end of the year will attain on an average a length of 29 mm.

These figures are of course only roughly approximate and are valid only for the particular locality where the limpets grew. Limpets at the Southend of Arran seem to reach a length of only 17–18 mm. by the month of July.

Second Year-Group.—Given the first year-group it is a simple matter to determine the second year-group. On December 31st, 1908, the first year-group had a certain range and a certain mean value, and the second year-group must necessarily have had on December 31st, 1907, approximately the same range and the same mean value. The limpets assigned to the second year-group (Nos. 40–65) have been selected on this principle. Their range of size on December 31st, 1907, is from 22 mm. to 34·4 mm., and their mean 28·8 mm. The mean value of the first year-group on December 31st, 1908, was 29·1 mm. and the range from 24·5 mm. to 33·8 mm., but if No. 7 had survived till December 31st the range would have been from about 21·5 mm. up to 33·8 mm. The average size on December 31st, 1908, in this year-group is 38 mm.

Subsequent Year-Groups.—It is not possible to arrange the limpets of 35 mm. long and upwards in year-groups with any certainty. The arrangement adopted above seems the most satisfactory, but it is only tentative.

3. *Variation in Rate of Growth with Increase in Size.*

The rate of growth decreases with increase of size. This fact is shown by the data already given, but in order to gain a precise knowledge of the manner of the decrease it is necessary to discount the possible influence of time of year and temperature upon the rate of growth. This has been done by taking the figures given in Table I., for the period July 30th to September 2nd, and considering along with them some other additional data which have reference also to the month of August. These are, (1) observations on the growth of 10 limpets at the Cloch, Gourock, from the end of July to the second week in September 1906 (43 days), and (2) on a similar number at the same place from July 31st to September 7th, 1907 (38 days). A few additional data referring to seven limpets at Kames, during July 1906, are also incorporated. The detailed observations are given in the following Tables.

TABLE III.

Growth during 43 *days. The Cloch, Gourock, Aug.* 1906.

Group.	Original size.	Final Size.	Growth per cent. in 30 days.
20—25 mm.	20·6	25·5	16·59
	21	27	19·93
	23·4	27	10·73
25—30 mm.	25	27·7	7·53
	26	29·5	9·41
	26·5	28	3·95
	27	31·2	10·85
40—45 mm.	42·2	45·5	5·46
	44·6	45	·62
45—50 mm.	46	46·5	·76

TABLE IV.

Growth from July 31 *to Sept.* 7 (38 *days*). *The Cloch, Gourock.*

Group.	Original Size.	Final Size.	Growth per cent. in 30 days.
15—20 mm.	16·4	21·9	26·48
	18	21	13·16
	19·8	23·5	14·75
35—40 mm.	39·1	43·6	9·08
40—45 mm.	42·5	43·5	1·85
	43·5	45·7	3·99
45—50 mm.	46·2	47	1·37
	46·5	47·5	1·69
	46·8	47·4	1·01
	49·7	50	·48

TABLE V.

Growth during July 1906 *at Kames, Kyles of Bute.*

Group.	Original Size.	Final Size.	No. of days.	Growth per cent. in 30 days.
0— 5 mm.	4	5	25	30·00
5—10 mm.	5·5	6	25	10·91
	8·5	10·5	31	22·77
10—15 mm.	10	13	25	36·00
	13	15	25	18·46
	11·5	13	31	12·62
	12	12·5	31	4·03

The observations recorded in Table I. amount to 42 for the month of August.

The mean values calculated are given in Table VI.

TABLE VI.

Rate of Growth and Size.

Group.	No.	Growth per cent. in 30 days.
0— 5 mm.	1	30·00
5—10 ,,	2	16·84
10—15 ,,	5	19·20
15—20 ,,	12	15·56
20—25 ,,	17	12·42
25—30 ,,	11	6·89
30—35 ,,	5	5·05
35—40 ,,	5	4·77
40—45 ,,	6	2·71
45—50 ,,	5	1·06
	69	

The percentages in the first two groups cannot be taken into account since the numbers are so small. From 10 mm. on to 25 mm. there is a gradual and uniform falling-off in the rate of growth. In the 25–30 mm. group there is a sudden fall of the rate to little more than half what it was at 20–25 mm., then there is another gradual decrease up to the length of 50 mm. There is a second slightly marked fall at a length of about 40 mm.

4. *Seasonal Variation in Rate of Growth.*

That the limpet grows more quickly in the warmer months of the year is a fact which is clearly shown by the data in Table I. In the first year-group for example, during the months of June, July, and August, the monthly increment of growth is about 3 mm. During September the increment is 2·2 mm., during

October 1·1 mm., during November ·6 mm., and during December ·7 mm. The percentage increase falls even more rapidly.

But it is in the second year-group (where there is little variation in the rate of growth due to age) that the seasonal variation is shown most clearly. During the first three months of the year growth is practically at a standstill, then during the summer a slow increase in size is manifested, but after October growth almost ceases again. It should be remarked in passing that the jump from 33·7 mm. at July 30th to 36 mm. at September 2nd does not signify that growth is specially active during August. The increase is due to the introduction into the group on September 2nd of the large shell No. 65 and to the reappearance of No. 64.

The seasonal variation in the rate of growth may be proved in another way. In Table VI. the percentage growth during the month of August is tabulated for limpets of all sizes.

It is easy to calculate from these data the number of days which a limpet would take to grow from 10 mm. to 15 mm., from 15 mm. to 20 mm. and so on, if it grew as quickly during the other months of the year as it does during August. Using the formula

$$O\left(\frac{100 + P}{100}\right)^n = F,$$

where O = original length, F = final length, P = percentage increase per 30 days, and n = number of months (of 30 days) taken to grow from O to F, we obtain the following results:—

Time taken to grow	*Days.*	*Sums.*
from 10 mm. to 15 mm.	69·26	69·26
15 „ 20 „	59·71	128·97
20 „ 25 „	57·18	186·15
25 „ 30 „	82·08	268·23
30 „ 35 „	93·87	362·10
35 „ 40 „	100·77	462·87
40 „ 45 „	132·15	595·02
45 „ 50 „	306·33	901·35

Suppose we start with a shell which is 10 mm. long on January 1st. If growth during the first two or three months is as rapid as it is during August, the shells in the first year-group should be 15 mm. long on March 10th, 20 mm. long on May 9th, 25 mm. long on July 5th. But actually, as is shown in Table I., they reach a length of 15 mm. only by the end of May, and 20 mm. some time towards the end of July. Hence growth during late winter and early spring is slower than during autumn. The same method might be applied to show that growth is again retarded on the approach of winter, but one more application of the method will suffice. If we take the second year-group and start with a shell 30 mm. long on January 1st, it will, if it grows at summer rates, reach a length of 35 mm. on April 4th,

40 mm. on July 14th, and 45 mm. on Nov. 23rd. But actually the second year-group attains to a length of only 38 mm. even by December 31st.

5. *Rate of Growth and Reproduction.*

We have seen that the variations in the rate of growth of the limpet's shell depend upon the age of the shell and upon the temperature. It is natural to enquire whether the attainment of sexual maturity has any marked effect upon the rate of growth. In other words, does arrival at a state of maturity coincide with any marked drop in the rate of growth? It would seem that it does, for sexual maturity is attained between 20 mm. and 25 mm., and there is a marked fall of the rate of growth at 25 mm. to half what it was at about 20 mm. Growth, however, continues for long after a length of 25 mm. is reached, and ceases only at 50–60 mm. The average full-grown size is about 45–50 mm. The limpet shell therefore doubles its length after sexual maturity has been reached. This fact recalls the law of growth which Dr. Fulton has formulated for fish, that they "approximately double their size and increase their weight about eight times after they have reached sexual maturity." (4. p. 182.)

After the attainment of sexual maturity the shell becomes much thicker and more solid in build. This increase in thickness is no doubt correlated with its slower growth.

6. *History of the Growing Limpet.*

The facts detailed above enable us to form a mental picture of the life-history of the limpet once it has settled down upon the shore as a miniature adult.

It may come into existence at any time from July to January. Its larval existence lasts probably only a week or two and it settles down as a minute shell, one or two mm. in length. Growth is rapid during the autumn. By January the shell is on the average about 10 mm. long, and during January and February it grows say 2 mm. The rate of growth is then accelerated, and growth continues actively throughout the summer. In August or September the limpet, which is now 20–25 mm. in length, becomes sexually mature. The rate of growth, which has hitherto been anything from 12–20 per cent. per month, now falls abruptly on the approach of winter and after the ripening of the gonad. By the month of December the limpet is on the average 29 mm. long. Very little increase of size is manifested during the early months of the second year, but by April a slow growth sets in at the rate of 5–7 per cent. per month, which falls off after the summer is past to 1–2 per cent. and finally in the early winter months ceases almost completely. During this year the gonad has undergone profound changes, returning in the early spring to a state almost of primary indifference and gradually ripening as the summer advances. The gonad attains its full size in this

second year, at the end of which the limpet is about 38 mm. long. The sequence of events during the third year is probably very similar to what it is in the second. Growth is even slower, and the limpet may increase only 5 mm. in length. The limpet possibly becomes full-grown at the end of this third year or at the end of the fourth year—at a length of a little more than 45 mm. Growth is almost at a standstill during the fourth year, and shells of 48 mm. and upwards may exhibit for long periods no growth at all, so that their age may be considerably more than four or five years.

The distribution of lengths in a large random sample (Table II.) shows that the limpets are subject to a considerable degree of elimination, the numbers in the first year-group (say 9–23·5 mm. for the month of July) being much greater than the numbers for the second year-group (say 24–38·5 mm.). The third and subsequent year-groups are not shown separately by a random sample but merge into one another. The great number of shells 45–53·5 mm. long which occur in the sample show that growth at this size is practically stationary, for shells of this size represent several different year-groups.

It is of interest to compare the life-history of the Tortoiseshell Limpet, *Acmæa testudinalis*, as related by Willcox (**11**). It shows much analogy with that of *Patella vulgata*. *Acmæa testudinalis*, it should be mentioned, reaches a length of only some 20 mm.

The breeding-season in America lasts from the middle of April to the end of July. Boutan (**1**) says that "la ponte de l'Acmée a lieu en avril et en mai" on the French coast, and I have reason to think that the same holds for the *Acmæa* of the Clyde. Willcox finds that the young *Acmæa* are 4–5 mm. long in September and early October, and that they attain sexual maturity under 10 mm., probably after one winter.

In Plate XXXII. the first two rows show stages of about fifteen months' growth, the second and third limpets in the second row showing the size at which sexual maturity is reached. The first two in the third row show the size of second year shells, the second (38·5 mm.) being from two to two and a half years old. The first limpet in the fourth row is probably a little more than three years old, while the other two in the row are full-grown limpets at least four to five years old. The two in the bottom row are veterans, the last one (61·2 mm. in length) being the largest limpet I have ever collected.

II. Changes in Shape during Growth.

About 1000 shells were collected at random during July 1903 and July 1904 at the Southend of Arran, and the ratios of the various dimensions calculated for every shell.

Table VII. gives the mean ratios in each group; L stands for length, B for greatest width, H for height, Ab and Af are explained a few lines further on

Table VII.

Mean Ratios.

Group.	No.	$\frac{L}{B}$	$\frac{Ab}{Af}$	$\frac{L}{H}$	$\frac{H}{B}$
5—10 mm.	21	1·32	1·64	3·52	·375
10—15 „	109	1·29	1·57	3·66	·352
15—20 „	163	1·27	1·46	2·95	·431
20—25 „	91	1·25	1·44	3·33	·375
25—30 „	63	1·23	1·36	3·11	·395
30—35 „	68	1·21	1·34	2·87	·422
35—40 „	81	1 19	1·31	2·65	·449
40—45 „	115	1·17	1·26	2·45	·478
45—50 „	138	1·16	1·24	2·28	·509
50—55 „	122	1·15	1·22	2·16	·532
55—60 „	25	1·15	1·17	2·28	·504

As is shown in Table VII. very considerable changes take place in the shape of the limpet-shell during its growth from 5 mm. to 60 mm. long.

$\frac{L}{B}$.—The shell becomes gradually broader in proportion to its length, and this change is remarkably uniform from group to group.

$\frac{L}{H}$, $\frac{H}{B}$.—It grows higher in proportion to its length and in proportion to its breadth. This change is on the whole a continuous one, but a reversal of its direction in both cases takes place in the transition from the first to the second, from the third to the fourth, and from the second last to the last groups.

$\frac{Ab}{Af}$.—The distance in a straight line between the apex and the anterior margin (Af) becomes greater with great uniformity in proportion to the distance between the apex and the posterior margin (Ab). It does not follow that the apex shifts backwards. The changes in the position of the apex may be represented graphically if the successive values of the ratios $\frac{L}{H}$ and $\frac{Ab}{Af}$ are drawn to scale on a constant L. It appears from such figures that the apex of the shell shifts gradually backwards during growth from 5 mm. to 25 mm., and then remains practically stationary till a length of 55 mm. is reached, when it again shifts backwards.

Most of these changes can be directly inferred from the shape of a typical fully-grown limpet-shell. A small limpet-shell has the shape of a flattened excentric cone, and the apex is in such a young shell finely pointed and turned forwards. As growth proceeds the sides of the cone do not grow straight on, but begin to curve inwards slightly, so that by the time the shell reaches a length of 50 mm. its outline as seen from the side may be such as is shown in the Plate (last row). All good-sized limpet-shells show this "ingrowth" in the anterior and posterior regions of the shell, and also at the sides of the shell, for a similar "ingrowth" takes place there also. This general "ingrowth"

accounts for the decrease of the ratio $\frac{L}{H}$ and the increase of the ratio $\frac{H}{B}$. The change in the ratio $\frac{Ab}{Af}$ is chiefly due to the same cause, and especially to the fact, easily observed, that the "ingrowth" at the posterior margin is much greater in extent than it is at the anterior margin, whence it arises that Af becomes larger in proportion to Ab. In the three cases in which $\frac{L}{H}$ increases and $\frac{H}{B}$ decreases during growth from one group to the next, one must suppose that an "outgrowth" has taken place, caused probably by the formation of very large projecting ribs, or else that the apex of the shell has been abraded. The latter explanation is probably the true one for the 55–60 mm. shells, for such old shells are usually very much worn and eroded, especially towards the apex.

The change in the ratio $\frac{Ab}{Af}$ may possibly be due also in part to the unequal rates of growth of the anterior and posterior margins. There is some reason to think that the anterior margin grows a little quicker than the posterior. If one examine a well-preserved "smooth" shell (see 9. p. 868) from above, one sees numerous fine ribs radiating from the apex. Now it very often happens that many of the lateral ribs curve slightly forward, while the anterior and posterior ribs run out in a straight line from the central apex. This shows that during growth the mantle (or the whole limpet perhaps) gets shifted forward a little relatively to the apex, and that accordingly the growth of the anterior margin becomes somewhat greater in proportion to that of the posterior margin. The ribs of the shell end in little projections of the rim, and to these projections of the rim correspond little projections of the edge of the mantle, hence from a curving forward of the ribs one can infer a movement forward of the mantle relatively to the shell-apex.

In addition to the radiating ribs there are visible on unworn shells numerous lines of growth. These are often very distinct, especially at about the level corresponding to lengths of 15 mm. and 30 mm. The shell lying between these two levels is probably added during the first summer and autumn's growth. It is, however, hardly possible to recognise annual lines of growth on the shell other than these two.

Shells of 40 mm. and more are usually very much worn on the upper part, from a level of 30 mm. upwards.

Besides the changes in shape during growth there is also a marked change in the build of the shell. It becomes very much thicker and heavier. This increase in thickness (out of proportion to the increase in length) becomes noticeable from a length of about 25–30 mm. onwards, *i. e.* in one year old shells and older ones. The rim becomes considerably thickened, and a great deal of shell-material is laid down inside the apex, which soon becomes solid to quite a considerable depth. In a limpet of 60 mm. the thickness of the shell at the apex was so great as 10 mm.

Throughout all these changes there persists a great uniformity. The relation that L > B > Ab > Af > H had no exceptions in the one thousand and three shells measured, except that occasionally in small shells B equalled Ab. The apex is always nearer to the anterior margin than to the posterior margin. The greatest breadth is invariably behind the apex, and usually behind the middle point of the shell, so that the outline of the margin is not an ellipse. Some results published by Malard (7) are obtained upon the assumption that the outline of the shell-margin may be treated as an ellipse. The index of ellipticity is calculated for several subspecies of *Patella*, and also an index of height. It does not appear that any allowance was made for the differences in the ratio of length to breadth and of each to height, which are found in shells of different lengths. For a form collected at Barfleur the index of ellipticity was ·6908; the curve of frequency was asymmetric and of Type I. Malard's inference that in this case selection was more pronounced in one direction than the other is quite unjustified.

The question naturally arises, are these changes in shape simply due to "laws of growth," or are they brought about by selection? It seems fairly certain that the changes in the ratios of the various dimensions of the shell are not due to the action of a process of natural selection, and that for two reasons: first, the changes are perfectly continuous and gradual from stage to stage; second, they are exhibited by every shell without exception. If the changes were due in any marked degree to the action of natural selection, a process of differential destruction must have been active at all stages, and one would expect to find dead shells which did not exhibit in their shape the changes which all good-sized limpets show. But such shells are not to be met with.

It can indeed be proved directly that the changes in shape may take place without the action of natural selection. For instance, 76 shells of 40–45 mm. length were collected at the Cloch, Gourock, and the mean breadth at a length of 40–42·5 mm. was calculated. The value obtained was 35·1448 mm., and the ratio of length to breadth was 1·174. The mean breadth at a length of 15–17·5 mm. was also calculated from measurements of 50 to 60 of these shells, advantage being taken of the lines of growth visible on the shell. (A few shells 38–40 mm. in length, collected at the same time as the 40–45 mm. set, were measured in order to make up the number to 60.) The ratio of length to breadth at this length was 1·26. The ratio of length to breadth in 60 shells 15–17·5 mm. in length collected at the same place and time as the large shells was 1·24. Now within the group composed of the 60 large shells natural selection has not acted, for natural selection acts by elimination, and there has been no elimination within the group. It is true that selection may have been at work before the length of 15–17·5 mm. was reached, and that these shells may represent a selected sample of the population below 15–17·5 mm. It is true also that natural selection may

have been at work on other shells 15–42·5 mm. in length—that possibility always remains. But for this group the action of natural selection between the lengths of 15 mm. and 42·5 mm. is excluded. Hence all the changes taking place during this period of growth are independent of selection. Now the values obtained for the ratio of length to breadth approximate very closely to those obtained for Groups 15–20 mm. and 40–45 mm. of the large series (Table VII.), and though the value for the breadth of the 40–42·5 shells at 15–17·5 mm. long (1·26) falls somewhat below the value of the ratio in Group 15–20 mm. (1·27), and might lead one to think that these shells were a selected lot, yet the value of the ratio for the 60 shells 15–17·5 mm. in length is even more divergent, being only 1·24. The differences are clearly due to the difference in environment, the series of which the ratios are tabulated in Table VII. having been collected in the Southend of Arran. One objection may be made to these results, and that is that shells of 40–45 mm. are usually very much abraded towards the apex, and consequently the measurements made on them at a length of 15–17·5 mm. cannot be depended upon. This objection has some weight, and to corroborate my results I have made measurements of 100 "smooth" shells 25–35 mm. in length (75 of them being 25–30 mm. long), which were carefully selected from over two hundred very kindly collected for me by Mr. David Baird, M.A., from the shore where my original set of 1000 had been gathered. The shells selected were those which had suffered practically nothing from weathering, and I am certain that the results they give are not appreciably influenced by the effects of abrasion and erosion. The ratio at a length of 15–17·5 mm. on these shells was 1·22, and at a length of 24–26·5 mm. it was 1·19. The change in this ratio may quite certainly be set down to a "law of growth" and not to selection. This change comes about in approximately four months' time.

Summary.

(1) The breeding-season extends from July to January.
(2) Sexual maturity is reached at a length of 20–25 mm.
(3) An average size for a limpet of the last season's brood in January or February is 10 mm. At the end of the first year it may be 29 mm. long. Probable sizes at the end of the second and subsequent years are 38 mm., 44 mm., 48 mm., 53 mm. Shells over 50 mm. may be considerably more than five years old.
(4) Sexual maturity is reached in the first year, and when the limpet is only half-grown.
(5) The rate of growth decreases with age and maturity. It is slower during the colder months of the year.
(6) Considerable changes take place in the ratios of the shell-dimensions during growth.
(7) These changes are probably in large part the expression of "laws of growth," and not due to natural selection.